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UPON THE OCELLUS FUNCTION OF THE SUBSPORANGIAL SWELLING OF PILOBOLUS.

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As is well known, the sporangiophore of Pilobolus shoots away its sporangium to a distance of several feet and therefore acts as a gun. The gun consists of three parts: (1) a basal reservoir which is at first densely filled with protoplasm and which, with the aid of rhizoids, serves to fix the gun firmly to the substratum, (2) a slender cylindrical stipe several millimetres long, and (3) a large oval subsporangial swelling. The shape of the stipe and of the subsporangial swelling is like that of an inverted Florence flask. The projectile—the sporangium—is seated on the free end of the subsporangial swelling, is discoid, is covered with an intensely black membrane, and contains many thousands of spores. *Pilobolus Kleinii* and *P. longipes* can both shoot their largest sporangia vertically upwards to a maximum height just exceeding six feet and to a maximum horizontal distance just exceeding eight feet.

When discharge of a sporangium takes place, the neck of the subsporangial swelling just beneath the sporangium is ruptured transversely, the wall of the swelling and of the stipe contracts elastically, and the cell sap is squirted out of the top of the swelling so that the sap carries the sporangium with it through the air. Hitherto, the swelling has been supposed to function merely as part of a squirting apparatus.

The subsporangial swelling of Pilobolus functions not merely as part of a squirting apparatus *but also as an ocellus* which receives the heliotropic stimulus which causes the stipe to turn the fungus gun toward the light. The swelling is transparent and refracts light like the bulb of a Florence flask filled with water. Its diameter is always greater than that of the black sporangium which it supports.

When the sunlight strikes upon one side of the swelling, the light rays are refracted through it and converge so as to form a spot of light on the other side. When the incident rays of light strike the sporangium head on and are exactly parallel to the long axis of the swelling, the spot of light which is formed by the rays entering that part of the swelling which bulges out beyond and around the sporangium, is symmetrically placed at the base of the swelling. Under these conditions there is physiological equilibrium and no heliotropic reaction takes place. When, however, the incident rays of light strike a swelling obliquely, the spot of light is placed on one side of the wall of the swelling in a manner which is asymmetrical for the swelling as a whole. Under these conditions, the protoplasm which is lighted by the spot of light, sends a heliotropic stimulus down to the protoplasm at the top of the stipe just beneath the base of the swelling. The top of the stipe then reacts by growing in length most rapidly on the side nearest to the spot of light and thus bending as a whole. As a result of this reaction, the swelling is moved about its base through an angle and the spot of light gradually passes downwards on the wall of the swelling until it comes to be symmetrically placed at the base of the swelling. As soon as the spot of light reaches this symmetrical position, a physiological state of equilibrium becomes established in the sporangiophore and the heliotropic reaction ceases. At the end of the turning movement the gun is directed toward the source of the brightest light.

In bright sunlight directed perpendicularly to the long axis of the swelling, the stipe of *Pilobolus longipes* was observed to turn the swelling and the sporangium through an angle of 90°, and thus complete its heliotropic reaction, in about one hour.

In *Pilobolus Kleinii* the protoplasm in the lower part of the subsporangial swelling and at the top of the stipe contains a red pigment; and, at the top of the stipe just above the stipe's motor region, the protoplasm is often heaped up in such a way as to form a strongly bi-concave, very red, centrally perforated septum. As shown by direct observations and by theoretical diagrams, this protoplasmic septum is admirably shaped and situated for receiving the light rays converging upon it when the gun is in a position of complete or almost complete physiological equilibrium. Its concave upper surface, its position with respect to the subsporangial lens, and its strong pigmentation which is especially marked on its upper surface, suggest a comparison in function with the retina of the eyes of certain Mollusca.

The diameters of the sporangium, the subsporangial swelling, and the motor region of the stipe below the swelling in a well-grown *Pilobolus Kleinii* were observed to be 0·43 mm., 0·76 mm.,

and 0·16 mm. respectively. A simple calculation based on these data shows that the sporangium, when head on to a beam of parallel light rays, casts a shadow which has an area 7·2 times that of a cross-section of the stipe. If there were no subsporangial swelling, the shadow of the sporangium would cut off the light from the top of the stipe before the ortho-heliotropic position had been completely attained. This would prevent the gun from being accurately directed toward the source of light. Evidently the difficulty of supplying the stipe with its required delicate heliotropic stimulus has been surmounted in the course of evolution by the intercalation between the sporangium and stipe of the large light-collecting subsporangial swelling. That part of the swelling which bulges out beyond the black sporangium receives the light and concentrates it by refraction upon the base of the swelling, the asymmetrical position of the spot of light so produced providing the stimulus to which the motor region of the stipe can react.

A model for illustrating the Pilobolus gun in its relations with light can be made for demonstrations to an audience as follows. Take a Florence flask, fill it with water, stuff a smooth plug of cotton wool down the neck as far as the base of the neck and then close the mouth of the neck with a cork. To represent the opaque sporangium, stick a plano-convex mass of moulding clay covered with black tissue paper over the flat surface of the flask's base so as just to cover it. As a source of light use direct sunlight or a beam from the arc of a projection lantern.

(1) To imitate the condition of the Pilobolus gun when in a state of physiological equilibrium. Hold the flask in the beam of light with its long axis parallel to the direction of the incident rays and its black base facing the rays. It will now be found that the rays of light falling on that part of the flask's bulb which bulges out beyond the black base are refracted so that they converge within the bulb and brilliantly illuminate the cotton wool plug at the junction of the flask's bulb and neck.

(2) To imitate the condition of the Pilobolus gun when not in a state of physiological equilibrium. Hold the flask in the beam of light with its long axis making a considerable angle with the direction of the incident rays and so that the rays fall obliquely upon the flask's black base. It will now be found that the cotton wool plug is no longer brilliantly illuminated but that a spot of light is formed by the refracted light rays upon the side of the bulb.

(3) To imitate the movement of the spot of light down the side of the subsporangial swelling of the Pilobolus gun when the stipe, responding to a heliotropic stimulus, is turning the subsporangial swelling and sporangium through an angle. Hold the flask as just described, so that the spot of light is upon the

side of the bulb. Now turn the flask so that its axis gradually assumes a direction parallel to that of the incident rays. During this turning movement one can observe that the spot of light gradually moves down the side of the bulb until finally it takes up a perfectly symmetrical position on the cotton wool plug, the plug thus again becoming brilliantly illuminated.

(4) To show that if the cell-sap in the subsporangial swelling were replaced by air, the swelling would not act as a lens. Hold the flask in the beam of light as described in the first experiment. The light is refracted on to the cotton wool plug. Remove the water from the flask without removing the plug. Now hold the flask in the beam of light in the same position as before. The light is no longer refracted on to the plug.

Pilobolus lives in fields, etc., on the dung of herbivorous animals. By directing its guns toward the source of the brightest light, it is enabled to shoot its sporangia into open spaces and, therefore, away from the dung masses and on to grass and other herbage. The sporangia are very adhesive and, especially after they have dried, stick tightly to whatever they have struck. Heavy rain storms do not dislodge them. Herbivorous animals eat grass and sporangia together. The spores pass through the alimentary canal of cattle and horses unharmed and germinate in the solid excreta as soon as they have been dropped.

In the heliotropic reaction of Pilobolus which is caused by the asymmetrical position of a spot of light we have a clear proof of the theory, first suggested by Haberlandt*, that heliotropic reactions may take place in plants through ocellus action.

The sporangiophore of Pilobolus, as far as I am aware, is the only ortho-heliotropic plant organ known which takes up its positively heliotropic position owing to the possession of a special light-perceiving cell structure.

Pilobolus may be well described as a fungus with an optical sense organ or simple eye, and in using its eye for laying its gun, it appears to be unique in the plant world.

The above is an abstract of a paper read December 10, 1920, at Guelph at the second annual meeting of the Canadian Branch of the American Phytopathological Society and again on December 28 at Chicago before the Physiological Section of the Botanical Society of America. On the latter occasion the model described in the abstract was successfully used to demonstrate the lens effect of the subsporangial swelling to a large audience. A fuller description of my observations, accompanied by illustrations, is in preparation for the press.

The University of Manitoba, Winnipeg,
February 1st, 1921.

* G. Haberlandt, Die Lichtsinnesorgane der Laubblätter, Leipzig, 1905.